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Diversity and spatial heterogeneity of mangrove associated sponges of Curaçao and Aruba

Ellard R. Hunting[1,2], Rob W.M. van Soest[1], Harm G. van der Geest[2], Anne Vos[3], Adolphe O. Debrot[4]
[1]*Zoological Museum, University of Amsterdam, Mauritskade 57, P.O. Box 94766, 1090 GT Amsterdam, The Netherlands, E.R.Hunting@uva.nl*
[2]*Department of Aquatic Ecology and Ecotoxicology, IBED, University of Amsterdam. Kruislaan 320, 1098 SM Amsterdam, the Netherlands*
[3]*Department of Marine Ecology and Evolution, Netherlands Institute for Sea Research (NIOZ), P.O. Box 59, 1790 AB Den Burg, Texel, The Netherlands*
[4]*Carmabi foundation, Curaçao, Netherlands Antilles*

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Abstract

Sponges are major epibionts of mangrove roots in the Caribbean. Mangrove sponge communities in the Caribbean mainly consist of species that are typical to this habitat and community compositions often differ from those found on coral reefs nearby. Heterogeneity in species distributions between locations and within locations between roots is often reported. This study quantifies the diversity and abundance of mangrove associated sponges in the inner bays of Curaçao and Aruba and correlates variability of regional sponge diversity with environmental variables measured along the surveyed sites. Tannin concentrations vary between mangrove roots, and were correlated to sponge cover as a possible cause for habitat heterogeneity on a smaller scale. A total of 22 species was observed. Heterogeneity in species richness and abundance was apparent, and several sponge species were restricted in their depth of occurrence. Statistical data reduction suggests that sponge diversity may be partly explained by the distance towards adjacent reefs and to the degree of eutrophication, in which the latter is comprised of rate of planktonic respiration, total carbon and turbidity. Tannin concentrations did not determine within locality species heterogeneity as *a priori* postulated, but were positively related to sponge cover for reasons not yet elucidated.

Contents

Introduction

Mangroves form the dominant vegetation in tidal, saline wetlands along (sub-)tropical coasts (Chapman, 1976; Tomlinson, 1986). Mangrove forests are among the most productive ecosystems on earth (Lugo and Snedaker, 1974) and provide nursing grounds for fish (Nagelkerken *et al.*, 2002; Mumby *et al.*, 2004). The fauna associated with mangrove roots is diverse, including crustaceans, bivalves, fishes, ascidians, hydrozoans, bryozoans and sponges (Sutherland, 1980; Fransen, 1986). Mangrove sponge communities in the Caribbean mainly consist of species that are typical to this habitat and in most cases differ from coral reef sponge communities nearby. Despite the characteristic fauna, heterogeneity in species distributions between locations and within locations between individual mangrove roots is often reported (Sutherland, 1980; Bingham, 1992; Farnsworth and Ellison, 1996; Rützler *et al.*, 2000; Diaz *et al.*, 2004; Wulff, 2004).

Several studies have addressed the spatial variability in species richness and densities in sponge community composition between localities in the Caribbean region. These studies revealed that the distribution of species in the Caribbean may be governed by a combination of physical and biological

factors, including larval availability (Bingham, 1992), proximity towards adjacent reefs (Ellison and Farnsworth, 1992; Rützler *et al.*, 2000), turbidity (Ellison and Farnsworth, 1992; Farnsworth and Ellison, 1996), presence of predators (Pawlik, 1998; Wulff, 2000; Wulff, 2005), exposure to air (Rützler, 1995), competition among sponges (Engel and Pawlik, 2005; Wulff, 2005) and sub-optimal levels of abiotic variables (Wulff, 2004; Pawlik *et al.*, 2007). However, controversy exists regarding the degree to which biotic and abiotic factors may dominate and at what scales they effectively affect species distributions (Wulff, 2004, 2005; Pawlik *et al.*, 2007). Moreover, most studies that concern the complexity of sponge distributions in the Caribbean region were conducted at off shore cays in Belize, and few studies were carried out in Florida and Venezuela. Consistencies in correlations with environmental variables should be verified and supplemented with quantitative data of mangrove associated sponges at other Caribbean sites in order to gain a more reliable representation of sponge distribution patterns throughout the Caribbean.

Factors that influence sponge distributions on a smaller scale have barely been studied. Sponge distributions within sites can be patchy, in which neighboring roots can harbor different sets of species or may lack any epibiont while neighboring roots are fully covered. Large differences in the composition of the sponge community between roots have been attributed to low recruitment rates, limited larval supply and variable flow rates (Sutherland, 1980; Farnsworth and Ellison, 1996). The importance of competitive interactions among species that occupy the same root has been demonstrated in Florida. Some mangrove sponges secrete bio-active compounds that mediate overgrowth interactions by inhibition of sponge growth in some species and promotion of overgrowth in other species (Engel and Pawlik, 2000). These aspects contribute to the variability in sponge distributions among roots, but our current knowledge of the underlying mechanisms

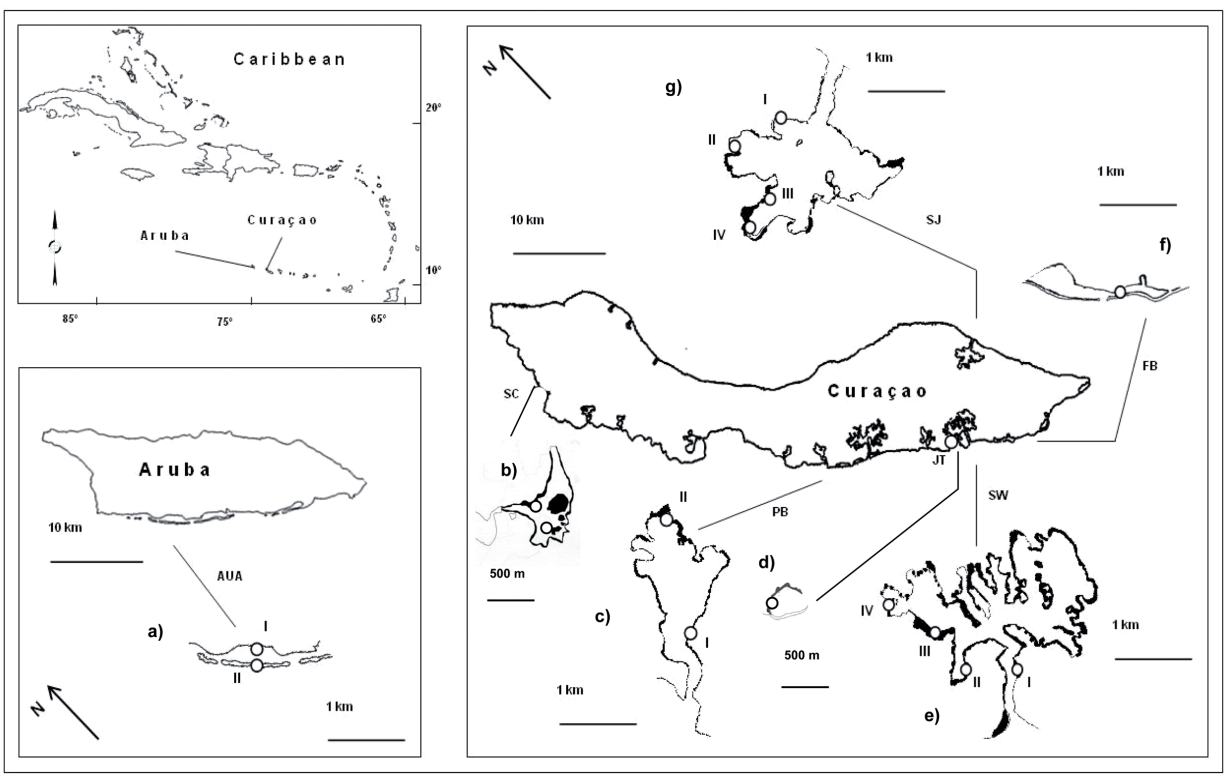

Fig. 1. Map of the Caribbean, Curaçao, Aruba and the inner bays. Localities are indicated with open circles and roman numerals, and mangrove fringes of Curaçao bays are shaded. Maps of bays and corresponding abbreviations: **a)** Aruba (AUA I-II); **b)** Boca st. Cruz (SC); **c)** Piscadera baai (PB I-II); **d)** Jan Thielbaai (JT); **e)** Spaanse Water (SW I-IV); **f)** Fuikbaai (FB) and **g)** st. Jorisbaai (SJ I-IV). Maps of bays taken from reports by I. Nagelkerken and E. Kardinaal.

steering sponge distributions on mangrove roots remains fragmented. Variability between roots is not likely caused by environmental gradients, since at this scale differences are too small to account for differences in the epibiont compositions of neighboring roots. In contrast, roots of the red mangrove, *Rhizophora mangle L* can have high and variable tannin concentrations (Tomlinson, 1986; Basak *et al.*, 1996). Tannins are a group of secondary metabolites that are known for their anti-microbial and anti-herbivore activity (Cameron and LaPoint, 1978; Alongi, 1987; Scalbert, 1991; Arnold and Targett, 2002, Erickson *et al.*, 2004), and it seems they adversely affect associated macrofaunal abundance (Lee, 1999). Ellison and Farnsworth (1996) reported the presence of mangrove-derived carbon in epibiontic sponges, suggesting that tannins may enter sponge-tissue and influence its physiology or larval settlement, and subsequently alter species distributions.

This study sets out to quantify the diversity of mangrove associated sponges in the inner bays of Curaçao and Aruba, and explores correlations between local environmental factors and sponge distributions. The inner bays of Curaçao and Aruba show minimal tidal fluctuations and are diverse in shape, size, accessibility and degree of wastewater disposal recruitment (Ebbing, 1997; Siung-Chang, 1997 and references therein), and are expected to differ in degree of nutrient pollution, turbidity and larval recruitment. Tannin concentrations of selected mangrove roots were compared to sponge cover and considered as a possible cause for within locality heterogeneity.

Material and methods

Study site

Several studies suggest that sponges are major epibionts of mangrove roots at the outer seaside fringing mangroves of Curaçao inner bays (Wagenaar Hummelinck, 1977; van Soest, 1978, 1980, 1984; Fransen, 1986), yet these data are non-quantitative. The mangrove associated sponges of Aruba have not yet been investigated. Several localities within bays of Curaçao and Aruba with fringing mangrove forests that were monopolized by the red mangrove *R. mangle* were investigated on the presence of sponges in April and May 2006 (Figure 1).

There is a greater magnitude of industrial waste loads (oil, grease, nitrogen, phosphorus suspended solids and biodegradable material) in Curaçao compared to Aruba (AUAI and AUAII: Vistalmar jetty and opposite) (Siung-Chang, 1997 and references therein). Within Curaçao there are differences between bays, i.e., St. Jorisbaai (SJI - SJIV) and Santa Cruzbaai (SC) show no signs of pollution, Fuikbaai (FB) and Spaanse Water (SWI - SWIV) are moderately eutrophicated, and Piscaderabaai (PBI and PBII) is highly eutrophicated (Ebbing, 1997).

Species diversity and richness

The methodology for determining sponge diversity and richness was modified after Ellison and Farnsworth (1992). Within the chosen localities, approximately 30-40 roots were haphazardly selected along a 50 meter transect. Roots were selected that submerged to a depth of at least 30 cm. Of these lengthier roots, every fifth root was selected for full characterization, i.e., length and diameter of the root, identification of sponge species, number of colonies and sponge coverage as percentage of total examined substrate. Sponge species that had not previously been encountered within a locality during the inventory were sub-sampled and stored in 70% ethanol for identification based on microscopic examination of skeleton structure and spicule morphology and following the nomenclature of Hooper and Van Soest (2002) and Rützler *et al.* (2007).

Vertical zonation

Depth of occurrence of sponge individuals was recorded in order to investigate the zonal distribution of sponge species. Zonation patterns were recorded as frequency of occurrence of all species present at depth intervals of 5 cm. Competition-related factors (i.e., overgrowth and allelopathy) may influence the local distribution of species and hence may interfere with other variables (e.g., light availability, grazing pressure) that might otherwise determine spatial patterns. In an attempt to exclude these competition-related factors, an additional assessment was performed in which sponge-species were recorded that either monopolized a root with considerable cover or dominated with at least 60% of the total sponge cover.

Environmental variables

Salinity was determined using a conductivity meter (Millwaukee, SM302), expressed in mS. Conductivity was converted to salinity following the Practical Salinity Scale of 1978 (PSS-78) (Lewis, 1980). Oxygen was measured with an oxygen electrode (OneCue-systems), read in percentage air saturation on a calibrated digital multimeter and pH was determined using a commercially available test (SeaChem). Turbidity was calculated measuring light intensities (I) at depth (z) and surface (0) using a photometric sensor read in mV by a digital multimeter. Obtained values were converted to the vertical extinction coefficient (η) following Lambert-Beer's equation: $I_z = I_0 e^{-\eta z}$. Nitrite (NO_2^-), nitrate (NO_3^-) and the total ammonia content (NH_{tot}) were determined using a commercially available test (SeaChem), and combined, representing dissolved inorganic nitrogen (DIN). Silicate (Si) was determined using a similar test. The concentrations of total organic carbon (TOC) and inorganic carbon (TIC) present in the water were quantified using a TOC-analyzer (model 700, O·I·Analytical). This type of analyzer acidifies TIC and oxidizes TOC to form carbon dioxide, which, in turn, is detected in a non-dispersive infrared analyzer (NDIR). Samples were stored as soon as possible at 4°C until analysis. Reaction time was extended to 35 minutes.

The rate of planktonic respiration was determined using an oxygen electrode (OneCue-systems), read in percentage air saturation on a calibrated digital multimeter. Water was sampled in plastic 1 L^{-1} bottles wrapped in aluminium foil to prevent oxygen production. Bottles were kept in the water to maintain *in situ* temperature. Decrease of oxygen concentrations was followed for one hour, in which a period of steady abating was used to calculate the rate of respiration.

Tannin analysis

The tannin content was determined for roots of *R. mangle* that were either fully overgrown with sponges or had no sponge overgrowth in order to test whether tannins relate to sponge presence. Five roots were sampled for each group in three different bays: Spaanse Water (SWII), Piscadera Baai (PBI) and Aruba (AUAI), and stored immediately at -20°C until analysis. All materials used for this analysis were wrapped in aluminium foil to prevent photo-oxidation. All chemicals used for this analysis were analytical grade or higher.

Tannin contents of the root samples of *R. mangle* were extracted from both the outer tissue, the periderm, and the remaining inner tissue. The periderm was ground in liquid nitrogen; the inner tissue was pulverized in a grinder (Janke & Kunkel, IKA-WERK) and subsequently ground in liquid nitrogen. Tannins were extracted as described by Hagerman (1988) using 0.5 mL 70% aqueous acetone on 100 mg sample and an extraction time of 100 minutes. Samples were subsequently assayed as described by Hagerman (1987). Extracts were put in 8 µL aliquots on Petri-dishes containing 10 $g.L^{-1}$ agar and 1 $g.L^{-1}$ Bovine Serum Albumin (BSA) fraction V (Merck, > 97%), dissolved in buffer consisting of 0.05 M glacial acetic acid, 60 µM ascorbic acid, adjusted to pH 5 with 2 M NaOH. Plates were incubated at 30 °C for 96 hours. Extracts diffusively migrated within the gel and tannins precipitated upon contact with BSA. The diameter of the resulting ring was measured, squared and expressed as albumin complexing capacity (ACC).

Statistical analysis

Similarity between localities was analyzed using a multivariate cluster technique, comprised of Euclidian distance and Ward's minimum variance amalgamation method (STATISTICA v.7.0.). Sponge diversity was expressed as the Shannon index $H`$, as this index subsumes species richness and abundance into a single value. $H`$ was subsequently related to environmental variables by performing linear regression on single variables and co-correlating variables grouped by principal component analysis (PCA) (SPSS® v.10.0.).

Data obtained in this study were simulated for sample-based rarefaction on algorithms provided by Ugland *et al.* (2003), which reveals differences in species density. Ecosim v.7.72. (Gotelli and Entsminger, 2006) was used to simulate individual-based rarefaction curves and the corresponding approximated 95% confidence intervals which allows for comparison between species-richness. Evenness (PIE) (Hurlbert, 1971) was also determined using Ecosim v.7.72. following the rarefaction principle, i.e., a random sample of individuals is drawn from a given species distribution to estimate sampling effects for the index and provides the probability that two randomly selected indi-

Table 1. Total abundance of sponges as percentage cover of the total examined substrate and corresponding biodiversity measures. Abbreviations of study sites (PB I-AUA II) as presented in Figure 1.

	Sponge-cover (%):							
Species	**PB I**	**PB II**	**SW I**	**SW II**	**SW III**	**FB**	**AUA I**	**AUA II**
Callyspongia (Callyspongia) pallida							0.45	
Chelonaplysilla erecta					0.16			
Chondrilla caribensis forma caribensis	2.47					1.26		
Clathria sp. indet.			1.95			2.27		
Clathria (Thalysias) raraechelae			2.93			1.04		
Desmapsamma anchorata			0.85					
Dysidea etheria			1.09	0.81	1.02	1.16	1.24	
Dysidea janiae			0.83					
Dysidea variabilis	1.65		0.11			1.67	0.35	
Geodia papyracea	9.2	0.52		3.98	1.67			
Halichondria (Halichondria) magniconulosa					0.14			
Halichondria (Halichondria) melanodocia						0.15	0.64	
Haliclona (Soestella) caerulea	0.19					0.28		
Haliclona (Rhizoniera) curacaoensis			0.04					
Haliclona sp. indet.							0.13	
Iotrochota birotulata						1.76		
Ircinia strobilina						2.55		
Lissodendoryx (Lissodendoryx) isodictyalis							0.87	
Mycale (Zygomycale) angulosa	0.73							
Mycale (Aegogropila) carmigropila	0.03		3.96		0.09			
Mycale (Carmia) microsigmatosa	1.6	0.41	2.01	3.17	1.82	0.1	0.32	
Tedania (Tedania) ignis	5.09	1.31	5.04	4.85	3.98	5.34	4.73	0.36
Shannon index	**1.523**	**0.964**	**1.930**	**1.111**	**1.432**	**2.032**	**1.496**	**0**
Total number of colonies	63	18	57	38	42	59	43	18
Total number of species	8	3	10	4	7	11	8	1
Total sponge cover (%)	20.96	2.24	18.81	12.81	8.88	17.58	8.73	0.36
Rarified species richness (n = 18)	5.63	2.96	7.42	3.94	5.60	7.85	6.45	-
95 % CL High	7	3	9	4	7	10	8	-
95 % CL Low	4	2	5	3	4	6	4	
Evenness (PIE)	0.93	0.59	0.85	0.79	0.30	0.68	0.98	-
Number of roots investigated	29	38	40	28	33	34	35	27
Investigated substrate area (cm^2)	9903	13516	14372	8870	9065	14969	12325	9351

viduals will belong to different species.

Zonation patterns were assessed performing a one-way ANOVA. Differences in tannin content in relation to sponge coverage were detected performing single *t*-tests. Inferential statistics were computed in Matlab v.7.0.

Results

Sponge diversity and richness

The inner bays of Curaçao and Aruba yielded a total of 22 sponge species at eight localities, which differed in number of colonies, species richness, percentage cover and composition of the community (Table 1).

Nineteen different species were found at Curaçao compared to eight at Aruba. Localities showing the higher diversity were Fuikbaai (11 species) and Spaanse Water (SWI - ten species; all localities of Spaanse Water combined yielded 13 species). Some species were regularly encountered (e.g., *Tedania (Tedania) ignis* (Duchassaing and Michelotti), *Mycale (Carmia) microsigmatosa* Arndt and *Dysidea etheria* De Laubenfels), whereas some species (e.g., *Chelonaplysilla erecta* Carter) were found only once during this inventory. No sponges were present in Jan Thiel Baai, St. Jorisbaai, Santa Cruzbaai and SWIV. Cluster analysis revealed variability in faunal composition among localities, whereas neighboring sites within the same bay did not cluster (Figure 2).

Except for Fuikbaai, all sample sizes (28-40

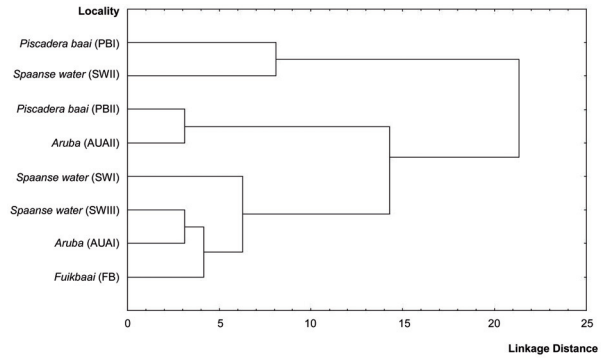

Fig. 2. Dendrogram of investigated localities based on Euclidian distance and Ward's method. Locations within bays are encoded as presented in Figure 1. Analysis presents 3 separate clusters in which sites located near each other do not cluster, thereby revealing local heterogeneity.

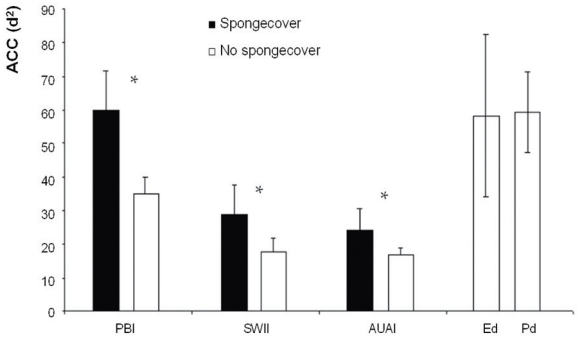

Fig. 4. Tannin contents of roots of *R. mangle* collected in Curaçao (PBI and SWII) and Aruba (AUAI) expressed as Albumin Complexing Capacity (ACC). Roots covered with sponges have consistently higher tannin concentrations, as compared with roots without sponge cover ($n = 5$ in all groups, asterisks indicate significant *t*-test statistics; PBI: $p < 0.01$; SWII: $p < 0.05$; AUAI: $p < 0.05$). There are no significant differences ($p = 0.95$) in tannin concentrations between the outer tissue, the periderm (Pd), and the remaining inner tissue (Ed).

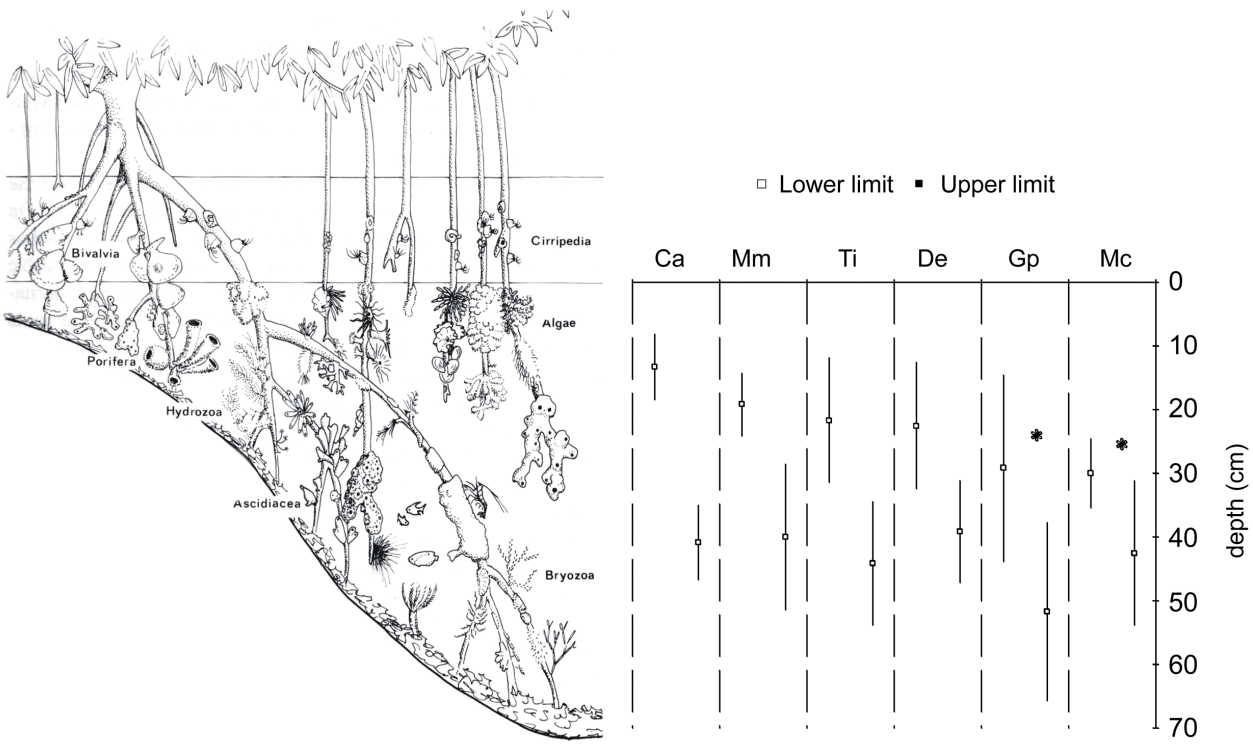

Fig. 3. Vertical distribution of six sponge species associated with mangrove roots focusing on sponge species dominating or monopolizing roots. Means are given with corresponding standard deviation**.** Regarding the upper limits of occurrence, two species (*G. papyracea* and *M. carmigropila*) are bound to deeper areas compared to the other sponges ($p < 0.05$, $n = 6$). Illustration of mangrove community is taken from Fransen (1986). Abbreviations: Ca, *Clathria* sp. indet; Mm, *Mycale (Carmia) microsigmatosa*; Ti, *Tedania (Tedania) ignis*; De, *Dysidea etheria*; Gp, *Geodia papyracea* and Mc, *Mycale (Aegogropila) carmigropila*.

Table 2. Single point measurements of environmental variables. n.d. = not determined.

Variable		Locality:									
		PB I	**PB II**	**SW I**	**SW II**	**SW III**	**SW IV**	**JT**	**SJ**	**FB**	**AUA**
pH	-	8.05	8	8.13	8	8.05	7	8.5	8.1	8.05	8.1
Oxygen	%	85	76	105	105	103	83	106	101	98	n.d.
DIN	$mg.L^{-1}$	0.12	0.15	0.08	1.1	0.2	3.8	0.3	0.2	0.0	0.6
TOC	ppm	1.804	1.949	1.738	1.917	1.756	3.440	2.175	3.285	1.852	1.740
TIC	ppm	27.23	27.45	23.93	23.41	22.69	25.68	26.02	26.16	23.59	25.17
RR	$\%O2.h^{-1}$	38	48	32	41	38	17	n.d.	n.d.	37	36
Si	$mg.L^{-1}$	0.5	2	0.6	0.4	0.4	0.4	0.2	0.4	0.2	0.4
Turbidity	η	1.65	1.65	1.68	1.67	1.67	1.66	n.d.	1.65	1.67	1.67
Salinity	psu	35.1	35.0	34.8	35.0	35.2	34.6	35.9	35.8	35.6	35.3
Distance	m	1150	2000	600	2200	2800	3800	100	2500	600	2500

roots) seemed adequate, as rarefaction curves revealed their asymptote (data not presented). Rarifying the data revealed differences in species density between most of the investigated sites and showed significant ($p < 0.05$) differences in species richness between several localities, including sites located within a single bay (Table 1).

Vertical zonation

Sponge species were more or less equally distributed over the examined root substrate if all sponge distributions were taken into account (data not presented). However, when competition related factors are excluded from the analysis (i.e., considering only roots monopolized or dominated by a single sponge species), differences become apparent for some species (Figure 3). These differences were significant ($p < 0.05$, n = 5) with respect to the upper limit of occurrence, in which *Geodia papyracea* Hechtel and *Mycale (Aegogropila) carmigropila* Hajdu and Rützler seemed restricted to deeper regions of the root. No differences were found with respect to the lower limits of their occurrence ($p = 0.35$, n = 5).

Environmental variables

Environmental variables are listed in Table 2. The localities differed greatly in their distance to the reef, dissolved oxygen levels and rate of planktonic respiration, and there were minor differences in turbidity, dissolved inorganic nitrogen and carbon. Sites were very similar in salinity and pH. Statistical data reduction by factor analysis suggests that species richness may be partly explained by distance to nearest reef and by eutrophication, in which the latter represents a linear combination of respiration rate (RR), turbidity and total carbon (TC) (statistics and equations provided in Table 3). Distance to adjacent reefs did not correlate with single or combined eutrophication components ($p > 0.8$). Turbidity, RR and TC partly co-correlated as revealed by principal component analysis, in which there was a clear relation between RR and sponge diversity, RR and turbidity, and turbidity and TC. There was no apparent relation between RR and TC, which caused the PCA-derived factor analysis to result in a single, insignificant factor.

Table 3. Statistics of single environmental variables and co-correlating variables grouped by PCA factor analysis for apparent correlations with sponge diversity.

Variables		**Statistics**			
Independent variable	Dependent variable	Linear fit		r^2	*p*-value
Distance to reef (*Factor analysis*)	Shannon index	-0.0321 ×	2.0531	0.5326	< 0.05
Turbidity	Total carbon	-147.88 ×	272.93	0.7537	< 0.05
Turbidity	Respiration rate	-314.81 ×	562.96	0.5176	0.068
Respiration rate	Shannon index	-0.0652 ×	4.0127	0.6918	< 0.05
Respiration rate	Total Carbon	1.3558 ×	2.5036	0.2787	0.21
Factor		-0.291 ×	1.9026	0.4262	0.113

Tannin analysis

Tannin contents of mangrove roots were significantly ($p < 0.05$) higher in roots that were covered with sponges compared to roots that were not covered with sponges (Figure 4). The tannin content was considerably higher in roots collected in the Piscadera Baai compared to roots sampled in the other bays (Figure 4). No differences ($p = 0.95$) were found between the tannin contents of the outer root tissue, the periderm (Pd), and the remaining inner tissue (Ed) (Figure 4).

Discussion

The majority of sponge species found in this study are typical mangrove sponges known to inhabit mangrove roots, seagrass beds and adjacent shallow reefs, whereas a few species are usually found in a reef environment. Most species found in this inventory were previously reported on mangrove roots in the Caribbean (e.g., Sutherland, 1980; Wulff, 2004). Species were patchily distributed within transects and several species that dominated at one site were completely absent at another site. This phenomenon is consistent with earlier reports on sponge community structures in mangroves (Rützler *et al.*, 2000; Diaz *et al.*, 2004; Wulff, 2004).

Results on environmental variables in this study reflect single point measurements and fail to reveal the temporal variation of these parameters, which may be large seasonally and even daily. Interpretations of apparent relations should therefore be restricted to environmental variables that show discernible gradients. Statistical data reduction suggests that the diversity patterns found in this study may relate to two variables: distance to the nearest reef and eutrophication.

The correlation between sponge diversity and proximity towards adjacent reefs validates earlier field observations in Belize, including an increased species richness with decreased distance to well developed coral reefs in off shore cays (Rützler *et al.*, 2000), and increased species richness in a coast to barrier reef transect (Ellison and Farnsworth, 1992). A similarity between this study and the Belizean survey of Rützler *et al.* (2000) is that localities close to reefs harbored more species typical of nearby reefs (*e.g. Desmapsamma anchorata* Carter, *Ircinia strobilina* Lamarck and *Iotrochota birotulata* Higgin), while localities further from the reef are largely comprised of species typical to mangrove habitats (*e.g. Tedania (Tedania) ignis, Lissodendoryx (Lissodendoryx) isodictyalis* Carter, *Haliclona (Soestella) caerulea* Hechtel, *Halichondria (Halichondria) magniconulosa* Hechtel).

Sponge larvae are incapable of traveling large distances and it has been demonstrated in Florida and Belize that epifaunal communities are partly structured by proximities to source populations and larval life span (Bingham, 1992; Farnsworth and Ellison, 1996). This may suggest that the reef partly functions as a larval pool, rather than that the mangrove habitat is self-sustaining. Sponge community composition varies or clusters with respect to proximity towards the reef (Figure 2) yet the clustering is not fully consistent. In some cases, localities close to the reef are more strongly related to localities that lie furthest from the reef, which points to mangrove-derived recruitment as well. This mechanism would parallel other areas (e.g., the Mediterranean), in which larval recruitment is also partly responsible for observed patterns in sponge community structures (Uriz *et al.*, 1998).

Although free-living phases of sponge larvae are short and dispersal abilities are limited, communities should be homogenously distributed after multiple generations. Distributions patterns are therefore controlled by a combination of factors. It has been shown by others that turbidity plays a pivotal role in structuring epifaunal communities (Bingham, 1992; Ellison and Farnsworth, 1992). In this study, statistical data reduction of combined parameters suggests a pattern of decreasing diversity with increasing eutrophication. Previous work has demonstrated the adverse effects of eutrophication on sponges under laboratory conditions (Roberts *et. al.*, 2006) and in other habitats, including reefs and kelps (Hindell and Quinn 2000; de Voogd *et al.*, 2006).

The importance of abiotic factors affecting sponge distributions in coastal and estuarine mangrove habitats has been emphasized in earlier studies, in which decreased species richness was attributed to large variation in temperature, salinity and tidal range (Ellison and Farnsworth, 1992; Rützler, 1995). In addition, transplantation of reef sponges to mangrove habitats was successful in off-shore cays with similar abiotic conditions in Belize (Wulff, 2005), but resulted in the death of transplants when

reef sponges were transplanted to coastal mangrove habitats and off-shore mangroves in Belize and Florida (Ellison and Farnsworth, 1992; Wulff, 2004; Pawlik *et al.* (2007). The inability of reef sponges to survive transplantation to coastal habitats has been attributed to sub-optimal levels of abiotic variables in coastal and estuarine mangrove habitats (Pawlik *et al.*, 2007).

The tannin concentrations of mangrove roots did not meet our expectation, as roots have significantly higher tannin contents when they are covered with sponges as compared with roots without sponge cover. In general, tannins are considered to function as anti-grazing substances, which may suggest that mangrove roots do not favour sponge coverage. However, another study provided evidence that this association is beneficial for roots, as epibiontic cover protects roots from isopod invasion, coinciding with increased growth rates of roots (Ellison and Farnsworth, 1990). In this study, roots were not examined on the extent of isopod presence, yet all sampled roots appeared rather fragile and soft to the touch, indicating that roots were damaged by isopods (Ellison and Farnsworth, 1990). Ellison *et al.* (1996) posed the presence of a facultative mutualistic relationship between the red mangrove and the sponge species *Haliclona (Reniera) implexiformis* Hechtel and *Tedania (Tedania) ignis*. They found a nutrient exchange between both organisms through fine rootlets, in which the sponge obtains organic carbon from the roots, and mangrove roots take up excretory nitrogen from the sponge. However, formation of such rootlets is restricted to only a few species (Ellison *et al.*, 1996) and the release rates of excretory nitrogen are highly variable between species and depend on the size of non-photosynthetic symbiotic bacterial populations and the nature of photosynthetic symbionts (Corredor *et al.*, 1988).

Although it is apparent that roots have increased tannin levels when covered with sponges, it remains unknown whether this increase has consequences for sponge physiology or the association, and whether tannins in roots of *R. mangle* are produced to act against sponge tissue. These aspects are subject of further investigation. There is evidence that the protein-binding potential of tannins is greatly reduced when the pH is greater than 7,5 (Martin and Martin, 1983, Martin *et al.*, 1985), and the pH always exceeded 7,5 at sites harbouring sponges during this investigation. The ineffectiveness of tannins under similar conditions has also been shown by Benner *et al.* (1986), who provided evidence that tannin leachates of mangroves did not reduce microbial degradation. In addition, the production of tannins as chemical defence by the brown algae *Fucus vesiculosus* sometimes fails to affect herbivores and it is hypothesized that other metabolites may be a confounding factor in identifying chemical defences (Kubanek *et al.*, 2004).

Alternatively, tannins may be redox active to metal ions and alter metal uptake, availability and toxicity, and the mangrove polyphenolics can have anti-oxidant properties (A.E. Hagerman, pers. comm., 2006). The greater part of the non-precipitating flavonoids in leaves of *R. mangle* is comprised of Quercetin, a compound highly effective in scavenging oxy-radicals (Kandil *et al.*, 2004). Tannin leachates may also provide a carbon source for sponges. An increased tannin content may then imply favourable conditions for sponges and larvae seeking a proper substrate to settle on and may favour roots with higher concentrations of tannins in the surrounding water. Future research efforts should elucidate whether increases in tannin concentrations are induced by newly colonizing sponge species or increased tannin concentrations in the surrounding water may act as a cue for attracting sponge larvae. This may provide more insight in the role of tannins in the distribution of mangrove associated sponges.

This study aimed to quantify diversity of mangrove associated sponges in bays of Curaçao and Aruba and to correlate complexity in community structure with environmental variables. Observed patterns validate earlier observations that a combination of physical and biological factors, proximity to source populations and water quality seem important in controlling epifaunal sponge distributions on a larger scale in Caribbean mangrove ecosystems. Heterogeneity in species distributions between roots remains unresolved in many aspects, although data presented here suggest that differences in tannin content may influence the structure of Caribbean sponge communities.

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